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A STATISTICAL STUDY OF *THAMNOPHIS BRACHYSTOMA* (COPE) WITH COMMENTS ON THE KINSHIP OF *T. BUTLERI* (COPE).

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The short-headed gartersnake has had a stormy taxonomic history. Originally described by Cope in 1892 from Franklin, Venango County, Pennsylvania, the name *brachystoma* was suppressed by Ruthven (1908), who, while noting that he lacked sufficient specimens to reach any position of certainty, considered it to be a synonym for *Thamnophis butleri* (Cope) 1889. Albert G. Smith reviewed the *butleri* complex in 1945 and decided that two distinct species were recognizable. For the more eastern of these he resurrected Cope's name *brachystoma.*

The Carnegie Museum took immediate steps to secure an adequate representation of this revived species, and at the invitation of Dr. M. Graham Netting, I began a statistical analysis of these specimens in 1947. Other duties forced me to lay aside this project, unfortunately, before its completion.

In 1949, Smith again considered the group, and this time reversed himself by deciding that *butleri* and *brachystoma* were subspecifically related, and that both were races of the plains gartersnake *T. radix.* Conant (1950) conclusively demonstrated that *radix* is specifically distinct from *butleri.* Conant (1950, 1951) further held that *brachystoma* shows no signs of intergrading with *butleri,* and that ''in view of the marked difference between them,'' they must be retained as discrete species. Conant premised his views on Smith's data, a key phrase to Conant's comments reading, ''—if Smith's data are accurate—.''

A number of unfortunate errors had crept into Smith's work, especially the 1949 contribution, which sharply limit its usefulness by leaving the reader uncertain as to what is valid and what is erroneous. In his first paper, for example, Smith reported (1945, 149) that in *Thamnophis brachystoma* the scales ''are almost always arranged in 17-17-17 rows,'' but in the second contribution (1949, 288, table 1) he omits the formula 17-17-17 entirely from his summary for *brachystoma* and instead states that 99.75% of his sample exhibit the formula 17-17-15. Changing his figures again, he reports on page 295 that 216 of his 221 specimens showed the formula 17-17-15 (216/221 = 97.7%, not 99.75%). But on

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page 297, he offers his reader a third choice by stating for *T. radix brachystoma,* under the heading *Diagnosis,* ''A gartersnake in which the dorsal scales are reduced to 17 rows *throughout*'' (italics mine)! Similarly, for *brachystoma,* he equates 4/221 on page 295 with 0.21% on page 288 (it should read 1.81%), 1/221 with 0.04%; for *butleri* 228/237 with 99.68% (instead of 96.2%), 7/237 with 0.29%, etc. In the consideration of *brachystoma's* supralabials (1945, 150) he refers to six individuals as constituting 0.04% of his sample, yet his sample numbers not 15,000 (as this value would require), but 221.

It is in the hope of clearing a path through this confusion that I have returned my attention to my old notes, and offer the following data.

Material and Methods

The sample reported upon herein is composed of 154 specimens, of which 110 are males, 34 are females, and ten are of undetermined sex. All are in the collection of the Carnegie Museum (C.M.), and were taken from the following Pennsylvania localities, which were among those previously mapped by Richmond (1952):

SPECIMENS EXAMINED:

CLARION: Strattonville C.M. 28156-66, 28169, 28171, 28233-37.

ELK: Portland Mills C.M. 28393-95; Pa. route 949, ½ mi. N. of the Jefferson Co. line C.M. 28397.

FOREST: E. bank of Allegheny River, 12 mi. N. of Tionesta C.M. 26851-84, 28131-36.

JEFFERSON: 5½ mi. N.E. of Sigel C.M. 28143-55, 28197, 28243; Cook's Forest C.M. 28954.

McKEAN: 4 mi. N.E. of Clermont C.M. 28740.

MERCER: 2-3 mi. N. of Grove City C.M. 28633.

VENANGO: 9 mi. E. of Oil City, near U.S. route 62 C.M. 27027-29, 27037; 1 mi. S.W. of President C.M. 27038-41; 1 mi. N.E. of Franklin C.M. 27732.

WARREN: *circa* 2½ mi. N.E. of Tidiute, near U.S. route 62 C.M. 26886-87, 27093; 11½ mi. N.E. of Tidiute, near U.S. route 62 C.M. 26888; 15 mi. N.E. of Tidiute, near U.S. route 62 C.M. 26889-98; 6 mi. W. of Warren, on the bank of the Allegheny River C.M. 27691-98; 4 mi. S.W. of Youngsville C.M. 27702; *circa* ¾ mi. N.W. of Pittsfield C.M. 27673-76, 27726-28; 4 mi. N. of Pittsfield C.M. 27710; 5 mi. N.W. of Pittsfield C.M. 27729; 6 mi. N. of Pittsfield C.M. 27734; 5 mi. E. of Columbus C.M. 27685-87; Benson's Swamp, 2 mi. E. of Columbus C.M. 27678; Sheffield C.M. 27505-12, 28662; 2 mi. S. of Sheffield C.M. 26899-916.

In addition to the foregoing, the following specimens were measured for total length only, and this value was applied in the preparation of table 3 (Growth and Age Groups):

CRAWFORD: Titusville C.M. 29870-71.

ERIE: 1 mi. E. of Corry, near U.S. route 6 C.M. 29881-82.

FOREST: 2 mi. N. of Tionesta, near U.S. route 62 C.M. 32232.

McKEAN: Morrison C.M. 29631; 6 mi. N.W. of Kane, near Pa. route 68 C.M. 29628.

VENANGO: "Ten Mile Bottom", 4 mi. N. of Van C.M. 32207-09; 2 mi. N.W. of Coal Hill C.M. 32199, 32201.

WARREN: Sheffield C.M. 29737-38 (A-G), 29796-802, 30042; Corydon C.M. 32238-40; 10 mi. S.W. of Warren, near U.S. route 62 C.M. 32245, 32247-49 (A-L), 32251-52 (A-H).

For statistical methods I have followed Arkin and Colton (1950), except for the coefficient of divergence which was introduced by Klauber (1940), and for Fisher's "t", which was taken from Snedicor (1946).

Scutellation

Dorsal Scale Rows

Unlike the sample *brachystoma* studied by Smith, where the number of scale rows was quite constant, the present series exhibits considerable variation (Table 1). Scale rows were counted one head's length behind the head, at midbody, and approximately a head's length anterior to the vent.

Table 1. Variation in number of dorsal scale rows

Scale row formula	f	Per cent of sample
17-17-17	118	76.7
17-19-17	17	11.0
17-17-15	13	8.4
17-17-16	2	1.3
19-19-19	1	0.6
19-17-17	1	0.6
18-18-17	1	0.6
17-18-17	1	0.6

Supralabials

In the present series, 90.3 per cent (139 individuals) possess six supralabials on each side of the head; 3.2 per cent (5) are bilaterally asymmetrical in having six on one side and seven on the other; 2.0 per cent (3) have six on one side and five on the other. Thus it is that 95.5 per cent of the sample have six supralabials on at least one side of the mouth. Of the remainder, 3.2 per cent (5) have seven of these scales on each side; 0.6 per cent (1) has five on each side, and one aberrant specimen (C.M. 27029) has seven on the left side of the head and six full labials on the right, with an additional small scale, which fails to reach the lip, interpolated between the fifth and sixth full scales. Should this scale be counted, this specimen would be added to those listed above bearing 7-7 supralabials; should it be ignored, the count would be 7-6. Counting supralabials in this species is complicated by the fact that many individuals have large labial-like scales continuing in series behind the last true supralabial. Therefore the arbitary rule was set that the posteriormost labial in contact with a temporal was the last one counted. Without such a criterion, one could defend several different supralabial counts for a single specimen.

Infralabials

In ascertaining the number of infralabials, the posteriormost scale having a point of contact with a supralabial when the mouth was closed was the last one counted, as again a series of labial-like shields extended behind the last true lower labial. Applying this rule, eight infralabials proved to be the number most frequently encountered, 35.0 per cent (54) showing this number bilaterally, 26.0 per cent (40) having eight on one side but seven on the other, 7.1 per cent (11) having the combination eight with nine, and 1.3 per cent (2) eight-six. Thus 69.4 per cent of the sample have eight infralabials at least unilaterally. Seven lower labials are born by 50.6 per cent of the sample in the following combinations: seven-seven, 19.5 per cent (30); seven-eight, 26.0 per cent (40); seven-six, 4.5 per cent (7); and seven-five, 0.6 per cent (1). Only 3.2 per cent (5) have six infralabials on each side; 1.3 per cent (2) shows the combination six-five; one specimen shows nine-nine and one, nine-ten.

Oculars

Less variation is displayed in the number of preoculars, where 81.2 per cent (125) have only one on each side, 11.0 per cent (17) have two on each side, and 7.8 per cent (12) show the combination one-two. The number of postoculars in *brachystoma* is commonly two or three, with 38.9 per cent (60) of this series having three on each side, 30.5 per cent (47) having two on each side, and 28.6 per cent (44) having the combination three-two. In two specimens (C.M. 26911, 28150) the postoculars on one side of the head are fused into a single high, curved scale. These two specimens show the formulae two-one and three-one. One lone example shows the combination three-four.

The wide range in the size of these various head scales, the large number of abnormalities and the subsequent variation in head scale counts impress one who is working with this species. Such wide variation is frequently encountered in small snakes and seems to be associated with a reduction of head size.

Ventral and Subcaudal Scutes

A summary of data regarding ventral and subcaudal scutes is presented in table 2. The ventrals of males are more numerous than those of females, the coefficient of divergence being 2 per cent. Notable sexual dimorphism is to be found in the number of subcaudals, where the males possess many more scutes (C.D. = 14.99%). The range in this character for males, from 63 to 75, only slightly overlaps the range for females, from 53 to 64. The subcaudal count proves to be the best single character for sexing individuals of this species. It has, of course, the advantage of remaining constant throughout the life of the snake, whereas the next best index for determining sex, the ratio of tail length to total length, is unreliable with small individuals. Since the terminal spine in *brachystoma* seems to include elements from both the left and right rows of subcaudals, this spine has been counted as a caudal on both sides.

A large number of unusual arrangements of ventrals and caudals was noted through this sample. Nine specimens have one or more caudals undivided at the midline, so that an entire ventral-like strap extends across the underside of the tail. In some of these specimens there are as many as five or six such anomalous caudals scattered among normally divided scutes. In two specimens, a number of the ventral plates are divided along the mid-ventral line, giving completely separated left and right elements. Their positions indicate that they are not merely the results of umbilical scars. In twelve more individuals there are similarly divided ventrals, but in these the situation is further complicated by the interpolation of a small additional scute on one side or the other which extends, caudal-like, only from the mid-ventral line to the first dorsal scale row. In eight more snakes, one or more ventrals is split crosswise, usually from one end to the mid-line, but sometimes even farther. It is remarkable, then, that 19.5 per cent (30) of this sample has some abnormality in the conformation of some of the ventral or subcaudal scutes. This may possibly suggest some instability in the genetic pattern of this form.

Throughout the sample the anal is entire, and the dorsal scales (with the exception of those in the first row on either side) bear weak keels.

Location of the Lateral Stripes

Many authors have pointed out the importance of the location of the lateral stripes as a key character in distinguishing between various members of this genus. Smith (1945, 140) has previously reported that in *brachystoma,* ''The stripes are on the 2nd, 3rd, and 4th rows anteriorly always, posteriorly it may be on 2 and 3.'' My observations differ sharply from Smith's. In the present sample, 87 per cent (134) possess the lateral stripe throughout the entire length of the body on scale rows two and three only; 6.5 per cent (10) have the stripe on row three and the adjacent portions of rows two and four at midbody, but only on two and three both anteriorly and posteriorly; 2.6 per cent (4) have the stripe on rows three and adjacent two and four through the anterior portions of the body, but only on rows two and three posteriorly; 1.9 per cent (3) retain the stripe on upper two, three, and lower four through the entire length; in two individuals the stripes are undiscernible; and in the remaining specimen the stripe is found on upper one, two and three in the anterior portions of the body, and on two and three only posteriorly.

Size and Growth

There have been no reports published from field studies on the growth of short-headed gartersnakes, and so deductions made from the present sample are of interest. In table 3, 194 snakes have been arranged in three groups according to the time of year in which they were collected. The last third of the growing season, from September 1, to the onset of the next growing season, in mid April, was selected as the first division. The first third of the growing season, from April 15 to June 30, composes the second division; the middle third, from July 1 to August 31, makes up the remaining section. Divisions between age groups are sharp and clear only in the first year, and then individual differences in growth rate befog the picture and permit only approximate partitions. It seems clear, however, that *brachystoma,* like many small snakes of temperate climes, approximately doubles its natal length during the first year of life, that it reaches mature dimensions at the end of the second year and then increases in length but slowly during its remaining life. It is also to be noted that the two sexes increase in length

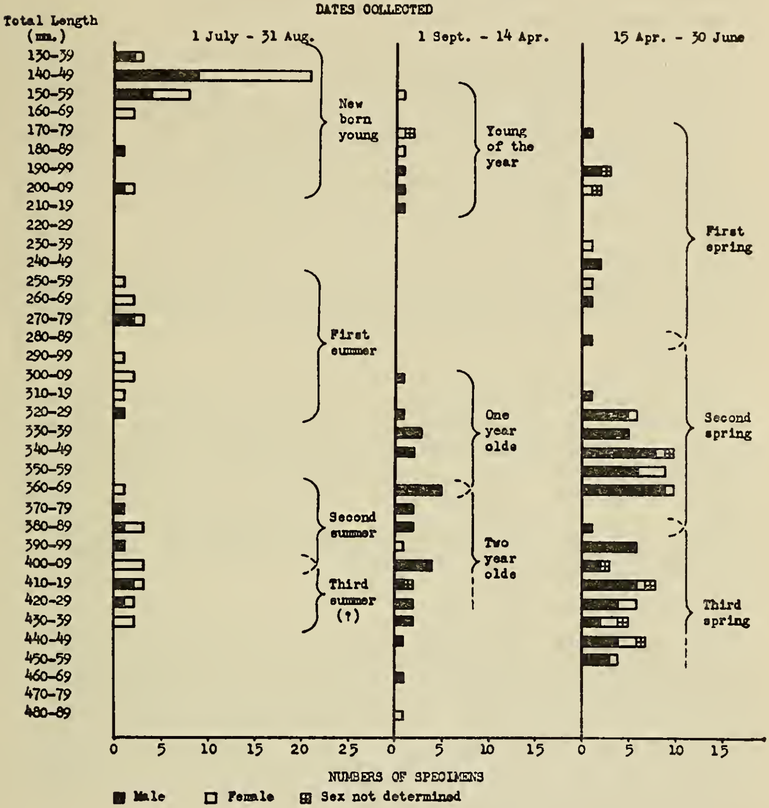
Table 2. Variation and sexual dimorphism in *brachystoma*

Character	Sex	N.	Min.	Max.	Mean	Standard Deviation	V.	Coefficient of Divergence (in %)
Ventrals	♂	112	134	144	139.12±.20	2.17±.14	1.56±.00	
	♀	33	131	140	136.36±.46	2.63±.32	1.93±.01	2.00
Caudals	♂	98	63	75	68.91±.27	2.67±.19	3.87±.01	
	♀	32	53	64	59.30±.43	2.43±.30	4.09±.03	14.99
Proportion of tail	♂*	91	23.2	27.7	25.95±.08	0.78±.06	3.01±.01	
(In % of total length)	♀	32	20.3	24.5	22.61±.18	1.00±.12	4.42±.01	13.76
Proportion of tail	♂*	91	31.6	38.4	35.03±.17	1.61±.12	4.60±.00	
(In % of BODY length)	♀	32	26.1	32.5	29.68±.32	1.83±.23	6.17±.07	16.53

*Only males with total lengths exceeding 230 mm. are included.

at approximately the same rate, and that no sexual dimorphism in size is apparent from these data.

Table 3. Growth and age groups



Smith (1945, 149) states that the largest specimen he examined was a female from near Tionesta, Forest County, Pennsylvania, which measured 506 mm., of which 118 mm. was tail. The smallest specimen in my study group is a male (C.M. 29802), collected on 17 August, 1951 at Sheffield, Warren County, Pennsylvania, which has a total length of only 135 mm. In three litters of new born young produced in the laboratory and preserved at once, the average length of the 12 males was found to be 146.4 mm., while for the 15 females the average was 146.0 mm. Two of these litters have already been mentioned by Richmond (1954, 257).

Comparison Between *brachystoma* and *butleri*

In the new light shed upon the situation by the foregoing, let us now reexamine Conant's thesis (1950, 76) that "In view of the marked difference between them, plus the fact that there is no evidence of an intergrading population, *bulteri* and *brachystoma* should be considered as distinct, although related, species.'' Conant considered this question in each of five areas, which we shall review in order:

Relative Head Width

Conant (*supra cit.*, 75) states, ''—its (*brachystoma's*) head is quite narrow and is not wider than the neck as is the case in *butleri.*'' Yet Smith (1945, 150), while deliberately seeking out differences to present in his paper separating the two forms, was forced to admit, ''The head size of both species was checked, and the difference in size of the head is so small that it is hardly recognizable as a distinguishing character.'' Conant, too, had written earlier (1938, 96) that in *butleri* the head was small and ''but little distinct from the neck.''

An examination of the two forms side by side suggests that the difference in head proportions is not so much one of width as of length. As Cope observed in assigning the specific name *brachystoma,* the head of this form is proportionately shorter than that of *butleri.*

Dark Spots

Conant (1950, 75) argues that ''In *butleri,* also, there *very often* is evidence of dark spots between the longitudinal stripes; these are lacking or only *faintly indicated* in *brachystoma.*'' In referring to these same spots in *butleri,* Conant (1938, 97) had previously noted that the spots are ''*obsolete in a majority of specimens,*'' even though ''readily apparent in others.'' (Italics mine.) Thus it is seen that in both forms the spots are absent from the pattern of the majority of specimens, or are only faintly indicated.

Number of Dorsal Scale Rows

In considering this character, Conant quoted Smith's 1949 contribution, which indicated that differential numbers of scale rows formed a sharp line of division between *butleri* and *brachystoma.* An examination of table 1 in the present paper will reveal that no such sharp line exists, but rather that the two populations gradually merge in this character; that 11.6 per cent of the *brachystoma* in the series under study possess 19 scale rows at midbody, an arrangement previously thought to be almost exclusively characteristic of *butleri.*

Number of Supralabials

The number of supralabials is six in 39 per cent of *butleri,* and seven in 57 per cent (Smith, 1945, 150). *Thamnophis brachystoma* is less variable in this regard, since 95.5 per cent of this study group bear six supralabials, and 6.5 per cent bear seven on one or both sides of the head.

Separation of Ranges, and Absence of Intergrades

Thamnophis butleri is regarded by Thomas (Conant, Thomas and Rausch, 1945, 67) as a pre-glacial ''endemic to the eastern part of the Prairie Peninsula—. It may be considered as a relict of a former climate—. It seems altogether likely that *butleri*—existed prior to the Wisconsin glaciation somewhere near its present range, as postulated by Schmidt (1938). Persisting throughout Wisconsin times beyond the periphery of the ice sheet, it may have spread into the glaciated portions of the Prairie Peninsula soon after the retreat of the ice.''

There is unanimity that *brachystoma,* like *butleri,* is a pre-Wisconsin endemic, and Netting is quoted by Conant (1950, 76) as being of the opinion that ''This snake may be a relict almost in situ, and—may have existed during Wisconsin times in essentially the same area which it now occupies.'' This is possible because, as Richmond's distributional report (1952, 315-16) so clearly demonstrates, *brachystoma* is almost entirely "restricted to one physiographic section, the (unglaciated) Allegheny High Plateaus Section of the Appalachian Plateaus Province.''

It is my belief, therefore, that before the Wisconsin glacial advance, *brachystoma* and *butleri* were members of a single species occupying a continuous geographical range, but the glacier's advance forced the main body of the species to retreat ahead of it to a point south of its terminal moraine, meanwhile leaving the segment of the population which has become *brachystoma* isolated in its high plateau locale. Due to pressures, competitive or climatic, *butleri* later migrated northward and has come to occupy primarily glaciated territory. That it has failed to reclaim all of its pre-glacial range should occasion no astonishment. As has been noted, it has failed by only about 90 miles to reclose the gap dividing it from *brachystoma.* Since the latter has remained virtually stationary during and since the Wisconsin, it likely is morphologically nearer the pre-glacial stock, whereas *butleri* has possibly evolved slightly more to fit it to the new demands of its glacier-modified habitat.

The belief that *butleri* and *brachystoma* were once one single form is supported by the fact that the most *butleri*-like *brachystoma* are those from the southern and southwestern borders of the present range, the area presumbably last in contact with *butleri.* Typical *butleri* characteristics (namely, scale rows 19 at midbody, seven supralabials, lateral stripes invading the fourth scale row) are possessed by more than twice as many specimens from this area as those from the remainder of the range. While this finding must at present be regarded as tentative due to incomplete sampling, the fact that one third of the southwestern *brachystoma* show one or more of these *butleri* characters is strongly suggestive, and were the two forms in geographical contact, it is possible that this section would be regarded as an area of intergradation.

For a summary of other points for comparison, see table 4.

Conclusions

Application of Fisher's ''t'' test to comparable sets of data from *butleri* and *brachystoma* demonstrates conclusively that the two constitute separate populations. The question as to whether they be two discrete species, or merely two races of a single species having discontinuous ranges is a moot point. It is clear that two races of one single species can exist with definite gaps separating their geographical ranges. Indeed, if our present concept of the mechanics of speciation is correct, it is inescapable that such a condition must sometimes exist. During the long period of time following the isolation of one segment of a population from others of its kind, while the gradual accumulation of changes in its genetic pattern is developing to the point where they

Table 4. *Thamnophis butleri* and *brachystoma* compared

	butleri		*brachystoma*
Character	Conant, 1938 (N = 39)	Smith, 1949 (N = 117 ♂♂ / 107 ♀♀	110 ♂♂ Present Sample (N ♀ 34 ♀= 10 undet.
Ventrals ♂	138-148 (142)	132-147 (140.4)	134-144 (139.1)
,, ♀	130-143 (137.5)	129-147 (137.9)	131-140 (136.3)
Caudals ♂	60-72 (66.5)	57-71 (64)	63-75 (68.9)
,, ♀	53-60 (56.6)	51-63 (56)	53-64 (59.3)
Preoculars	1	--------	usually 1, occasionally 2
Postoculars	usually 3, occasionally 2, rarely 1	normally 3, may be 2	commonly 2 or 3, rarely 1
Supralabials	6 or 7, rarely 8	--------	usually 6, occasionally 7
Infralabials	most often 8, occasionally 9, rarely 7 or 10	--------	commonly 7 or 8, sometimes 6, rarely 5, 9, or 10
Position of Lateral Stripe on Scale Rows	upper 2, 3 and lower 4 anteriorly, 2 and 3 posteriorly	involves 2nd scale row	usually 2 and 3 only; occasionally upper 2, 3, and lower 4
Tail length ÷ ♂ total length	23.0-26.2 (24.9%)	21.5-28.2 (24.8%)	23.2-27.7 (25.9%)
♀	21.4-23.8 (22.3%)	19.3-24.4 (21.6%)	20.3-24.5 (22.6%)

Figures in parentheses indicate the arithmetic mean.

are great enough to render it a recognizably distinct species, that population must of necessity belong to the species from which it has been isolated. The position of the final point of departure in such a situation, that point where the isolated population ceases to be conspecific with the parent stock, depends ultimately upon a subjective evaluation by the reviewer, colored by his own species concept. While caution must be exercised in the erection and continued recognition of species, it seems advisable in the absence of concrete contrary evidence to allow the present practice of regarding *butleri* and *brachystoma* as distinct species to continue unchanged.

Acknowledgments

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